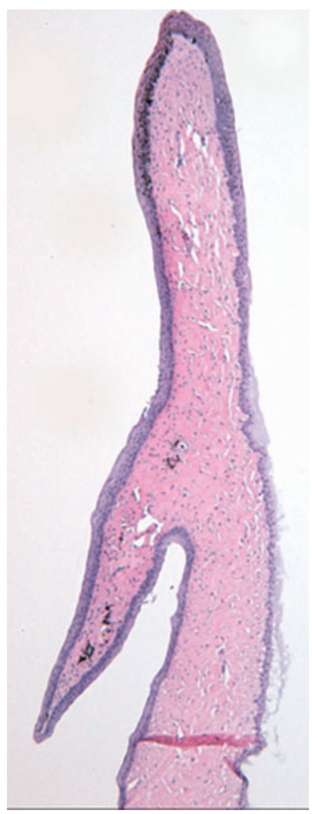
COVER ILLUSTRATION

The falcon's stoop

Ferocious speed in a predator is an admired, envied and, certainly, feared strategy. But, pure acceleration and speed have their own perils—problems which must be either solved or avoided for success. For example, the ocular surface will rapidly dry as the rush of wind evaporates the aqueous tear film, especially with the high speeds generated during the spectacular stoop of a falcon which approaches 300 km/hour. The disturbance of the ocular surface will challenge tear physiology, and the smooth surface essential for clarity of the image.

The nictitating membrane, or third eyelid, is unique to vertebrates, although not found in all groups. In many species, it represents the principal mechanism of ocular cleansing. In birds, the external eyelids possess smooth muscle, and may close only during sleep. The nictitans, on the other hand, is operated by two striated muscles and is capable of extremely rapid sweeps across the ocular surface to clear the cornea of debris. Ocular surface lubrication originates from two secretory glands. The lacrimal gland is situated in the inferior temporal quadrant associated with the more active lower eyelid, although in many species this gland is absent or rudimentary. Additionally, most birds, especially cormorants and falcons, have a second secretory gland called a Harderian gland located in the posterior and nasal aspect of the orbit associated with base of the nictitating membrane. In falcons, this secretory gland produces a viscous solution to moisten the cornea during the breathtaking stoops that are the falcon's trademark. Although the composition of these secretions is not known, a compound such as hyaluronic acid would moisten the surface without the rapid evaporation seen with a more dilute tear film. Such a coating would maintain a smooth surface, but might pose other difficulties by collecting debris.

The nictitating membrane of many such birds has a cartilaginous-like connective tissue fold along the leading edge of the membrane called the marginal plait. With each blink this flange-like flap (fig) collects the tear film and any associated debris to drain through the enlarged puncta into the nasolacrimal system. It is probably aided in this corneal cleansing role by a layer of "feather epithelium." This remarkable adaptation of a surface epithelium is believed to be unique to the epithelium lining the nictitans of many birds and reptiles. Long microvilli with club-like termini and numerous secondary projections from their long axis extend from the apical membrane of epithelial cells lining the bulbar surface of the third eyelid. Those seen here on the peregrine falcon (cover, left) are extremely robust and likely form a "histological feather duster" that sweeps the cornea clean with each darting excursion of the clear nictitans (cover, right).



Note marginal plait and feather epithelium along the edge.

Other visual problems are presented during the stoop though, and disturbance of the tear film is just the beginning. Falcons are bifovate with an infula between these two foveae (see *BJO* covers for October 2000 and February 2001). How is the image acquired and successfully visualised, especially during its stoop?

In falcons, the nasal fovea is deeper, steep walled (convexiclavate), and probably has better acuity, in contrast with eagles, which have a deeper temporal fovea. It is the temporal foveae in falcons that are capable of simultaneous image capture for stereopsis. The falcon uses its deeper nasal fovea to sight its avian prey from perhaps 400 metres in elevation. As the falcon begins its attack, it has a spiralling flight that allows it to keep the nasal fovea on the prey as long as possible even though it is not as direct a flight path (Tucker VA, *J Exp Biol* 2000;**203**:3745). Falcons use this spiral pathway to maintain the image consistently on the nasal fovea without tilting the head sideways during the stoop. Tilting would present the side of the head and increase aerodynamic drag. This technique does not force the bird to sacrifice acuity for stereopsis in the early phase of its hunt. But as the bird approaches its prey the flight pattern becomes more direct and the image swings from the nasal foveae to the temporal foveae via the infula, allowing the bird to maintain sharp acuity through the change in orientation of the image. Once the image has been transferred to the temporal fovea, stereopsis is achieved. Dramatic feats of acuity are not required at this stage in the hunt, but stereopsis is.

Furthermore, some falcons have been measured as having visual acuity of 75 to as high as 160 cycles per degree as compared to our 30 cycles per degree.

We have long realised these fascinating visual skills and have developed a unique relationship with falcons through falconry. Furthermore, falconers have recognised their own human visual limitations and often carried a caged shrike to alert the falconer when his bird was on the wing and returning from its hunt. The shrike would become agitated when the falcon was returning well before the falconer could see his bird, allowing the falconer time to prepare the jesses.

A successful falcon's stoop is one of the supreme and dramatic events in natural history and its witness is never forgotten.

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